

# Myrmecophagy by *Pseudochelidon eurystomina* and other African birds

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Received 10 March 1992

Feeding upon dangerously venomous prey such as Hymenoptera, scorpions and snakes must present birds with problems, the adaptive morphological and physiological solutions to which have not received a great deal of attention from ornithologists. Although ants (Formicidae), some other hymenopterans, and termites (Isoptera) are abundant in humid regions, birds that exploit them for food incur a further set of problems arising from their prey's swarming and patchy distribution. Some aberrant social and behavioural adaptations of such specialist bird species are already known and more may be expected to be found. For both reasons, physiological and sociobiological, myrmecophagy or ant-eating by birds should be of interest. This paper adds a swallow to the known 'professional' myrmecophages amongst African birds, and briefly reviews ant predation in African nonpasserine and several passerine families.

## *Pseudochelidon eurystomina*

The African River Martin *P. eurystomina* is an aberrant swallow or swallow-like bird generally placed in the hirundine subfamily Pseudochelidoninae, of which the only other species is *P. sirintarae*. The latter was discovered in 1968 and is known only from the few birds that wintered at Bung Boraphet reservoir in central Thailand 1968–1980; it has not been seen since (Turner & Rose 1989). Chapin (1953) provided the basis of knowledge about *P. eurystomina*, about which rather little is still known (Keith *et al.* 1992), although further observations have recently been made at a breeding colony near Animba, Port Gentil (0°58'S, 8°54'E), Gabon, September–October 1989 (Alexander-Marrack, in press). Its known breeding range is the middle and upper Congo River and the lower Oubangui River where it occurs from January to April–May, and near the coast of Gabon and Congo Republic where it occurs only from May/June to November, breeding September–October. There is some evidence of migration between the interior and coastal regions (Erard 1981).

The species is thought to forage exclusively on the wing, and its flight actions are reminiscent more of American *Progne* martins than of typical *Hirundo* swallows. Dense flocks fly with the co-ordinated precision of European Starlings *Sturnus vulgaris* (Brosset & Erard 1986); almost nothing else is known about the social organization of this swallow.

## Materials and methods

P. Alexander-Marrack made a small collection of faeces and regurgitates (pellets) at the Animba colony and enabled me to examine them.

TABLE 1.

Prey of *Pseudochelidon eurystomina*, Animba, Gabon, 1989: (a) faeces, 24 September, (b) regurgitates, 1 October, (c) regurgitates, 15 October

	(a)	(b)	(c)	Totals	%	Approx. no. of genera
Odonata	0	3	4	7	0.7	2
Isoptera	39	198	6	243	23.8	2
Heteroptera	1	1	1	3	0.3	3
Lepidoptera	0	1	0	1	0.1	1
Diptera	4	0	0	4	0.4	3
Neuroptera	0	0	1	1	0.1	1
Coleoptera	1	2	8	11	1.1	5
Formicidae	49	225	387	661	64.8	17
Other Hymenoptera	1	73	15	89	8.7	32
<b>Totals</b>	<b>95</b>	<b>503</b>	<b>422</b>	<b>1020</b>	<b>100.0</b>	<b>66</b>

Faeces are straight or curved cylinders 2.0–3.2 mm in diameter, found in pieces up to 9 mm long, consisting of densely-packed blackish sclerites in a sleeve of white crystalline uric acid. They were teased by hand and heated to 40°C in glycerol for 5 hours to dissolve the uric acid. Insect head capsules, mandibles, wings and some other recognizable fragments were sorted by hand and identified taxonomically by reference to the literature and insect collections at Sultan Qaboos University, Oman. Apart from loss of antennae, setae and some mouthparts, head capsules were rarely damaged; many even retained antennae and all mouthparts.

The regurgitates consisted of 10–12 ovoid or subspherical dry blackish pellets measuring 6–7 × 10–11 mm, and together weighing 1.4 g. They were moistened with ethanol and divided into 26 subsamples which were teased and sorted by hand in ethanol using a high-powered dissecting (binocular) microscope. After removal of insect head capsules, 5 subsamples were re-examined and the number of further head capsules recovered indicated that at least 95% of them had been recovered in the initial search.

## Results

Regurgitates and faeces consist entirely of insect remains. More than 1000 head capsules were recovered, in proportions of taxa that differed substantially between the 3 samples (Table 1). In total, ants compose about 65% of the diet of *P. eurystomina*, other hymenopterans 9%, termites 24%, and all other insect Orders only about 2%. A few almost entire ants present in pellets were identified from keys in Hölldobler & Wilson (1990) as species of *Camponotus* (Formicinae) and *Crematogaster*, *Monomorium* and *Pheidole* (Myrmicinae). Other ants were not identified to genera. At least 17 types or genera of ants were evident in the samples, but many of the 32 apparent taxa and 89 specimens of 'other Hymenoptera' may well have been ants also, to judge from descriptions of head capsules in Hölldobler & Wilson. 29% of the ants appeared to belong to a single (unidentified) taxon and 43% to 5 others.

Six whole ants were 6, 6, 7, 8, 9 and 10 mm long. Widths of ant head capsules, in relation to the head size and body lengths of the whole ants, suggested that the majority of ant prey were *c.* 8 mm long. Largest prey items were a damselfly (Odonata) probably > 30 mm long and a sphecoid wasp probably 13–16 mm long. At the other extreme, some hymenopteran heads were only 0.3 mm in width so that the whole insect may have been no more than 2 mm long; and an entire beetle was only 2.2 mm long.

### Predation on ants by African birds

Information on diets of birds in Africa has been obtained mainly by museum skin collectors, economic biologists studying waterfowl, gamebirds and agricultural pests, and ornithologists reporting on gizzard contents of road kills or analysing regurgitated pellets. The literature, which is large and diffuse, has been reviewed in *The Birds of Africa* (Vols 1–4: Brown *et al.* 1982, Urban *et al.* 1986, Fry *et al.* 1988, Keith *et al.* 1992), with accounts of 1187 species, including all of the nonpasserines and the passerines from Eurylaimidae to Myrmecocichla in Turdidae. There are *c.* 864 remaining passerines (*Monticola*, *Zoothera*, *Turdus*, warblers, flycatchers, sunbirds, shrikes, starlings, weavers, finches etc.), for which no data have been collected, and to that extent this review and Table 2 are incomplete. Neither primary literature sources, nor such essentially extra-African works as *The Birds of the Western Palearctic* (see especially Vol. 5, Cramp 1988), have been utilized. In the latter work, food data from Africa for species that visit or reside there are summarized in *The Birds of Africa*; food data from Europe are somewhat peripheral to this paper and in general have been ignored. Many taxa are not implicated in ant-eating at all: they are listed in the Appendix and, excluding 194 fully aquatic foragers, they represent 359 species.

Table 2 lists 116 genera, each with one or more species that eat ants. The genera include 622 African species, of which 272 eat ants—that is 28% of the terrestrial avifauna (359 + 622 species) reviewed to date. It is likely that most congeners of ant-eating species will eventually be found to eat ants also, occasionally if not regularly. In that event the proportion of myrmecophagous species in the terrestrial avifauna could prove to exceed 60%.

### Major ant predators

Fifty-five species are identified as major ant predators in Table 2 (quotations are from *The Birds of Africa*).

**PHASIANIDAE** *Alectoris barbara*: "Seeds, fruits and leaves, supplemented by insects, especially ants . . . food of young often mainly ants". *Francolinus lathamii*: "90% arthropods, especially termites *Basidentitermes* spp. and ants *Psalidomyrmex* spp.". *F. levaillantii*: 70–80% of the crop volume is vegetable matter, and the rest of the diet is "mainly ants, spiders, grasshoppers, millepedes and beetles". *F. capensis*: vegetable matter and "insects (especially termites and ants)". Phasianids in general and francolins *Francolinus* in particular appear to be important ant predators.

TABLE 2.  
Genera and numbers of species of African birds known to eat ants  
(from *The Birds of Africa* 1-4)

Family and genus	Numbers of species			Family and genus	Numbers of species		
	in Africa	known to eat ants	major ant predators		in Africa	known to eat ants	major ant predators
NON-PASSERINES							
THRESKIORNITHIDAE				CAPRIMULGIDAE			
<i>Threskiornis</i>	1	1		<i>Caprimulgus</i>	21	7	
<i>Geronticus</i>	2	1		<i>Macrodipteryx</i>	2	2	
PHASIANIDAE				APODIDAE			
<i>Agelestes</i>	2	1		<i>Rhaphidura</i>	1	1	
<i>Guttera</i>	2	1		<i>Telecanthura</i>	2	2	
<i>Numida</i>	1	1		<i>Neafrapus</i>	2	2	
<i>Coturnix</i>	3	2		<i>Schoutedenapus</i>	2	1	
<i>Alectoris</i>	2	1	1	<i>Cypsiurus</i>	1	1	
<i>Francolinus</i>	36	8	3	<i>Apus</i>	11	8	
TURNICIDAE				<i>Tachymarptis</i>	2	2	
<i>Turnix</i>	2	1		COLIIDAE			
RALLIDAE				<i>Colius</i>	4	1	
<i>Himantornis</i>	1	1		ALCEDINIDAE			
<i>Canirallus</i>	1	1		<i>Halcyon</i>	9	2	
<i>Sarothrura</i>	7	3		MEROPIIDAE			
<i>Crex</i>	2	2		<i>Merops</i>	18	10	3
OTIDIDAE				CORACIIDAE			
<i>Neotis</i>	4	2		<i>Coracias</i>	6	3	
<i>Chlamydotis</i>	1	1	1	<i>Eurystomus</i>	2	2	2
<i>Eupodotis</i>	9	2		PHOENICULIDAE			
GLAREOLIDAE				<i>Phoeniculus</i>	8	5	
<i>Cursorius</i>	6	1		UPUPIDAE			
<i>Glareola</i>	5	1		<i>Upupa</i>	1	1	
CHARADRIIDAE				BUCEROTIDAE			
<i>Vanellus</i>	14	5		<i>Tockus</i>	14	6	
LARIDAE				<i>Ceratogymna</i>	7	4	
<i>Larus</i>	20	3	1	CAPITONIDAE			
<i>Chlidonias</i>	3	1		<i>Stactolaema</i>	4	1	
PTEROCLIDAE				<i>Pogoniulus</i>	10	1	
<i>Pterocles</i>	12	1		<i>Tricholaema</i>	6	1-2	
COLUMBIDAE				<i>Lybius</i>	12	3	
<i>Streptopelia</i>	11	1		<i>Trachyphonus</i>	5	2	
CUCULIDAE				INDICATORIDAE			
<i>Cuculus</i>	6	1		<i>Indicator</i>	9	6	
<i>Cercococcyx</i>	3	1		PICIDAE			
<i>Centropus</i>	7	2		<i>Jynx</i>	2	2	2
STRIGIDAE				<i>Campethera</i>	10	10	10
<i>Glaucidium</i>	5	1		<i>Geocolaptes</i>	1	1	1
				<i>Dendropicos</i>	12	4	
				<i>Picoides</i>	3	1	
				<i>Picus</i>	1	1	1

Continued on next page

TABLE 2. (cont.).

Family and genus	Numbers of species			Family and genus	Numbers of species		
	in Africa	known to eat ants	major ant predators		in Africa	known to eat ants	major ant predators
PASSERINES							
PITTIDAE				PYCNONOTIDAE			
<i>Pitta</i>	2	1		<i>Andropadus</i>	11	5	
ALAUDIDAE				<i>Baeopogon</i>	2	1	
<i>Miraфра</i>	21	3	1	<i>Ixonotus</i>	1	1	
<i>Certhilauda</i>	5	4	2	<i>Thescllocichla</i>	1	1	
<i>Pinarocorys</i>	2	1		<i>Phyllastrephus</i>	17	5	1
<i>Chersomanes</i>	1	1		<i>Bleda</i>	3	3	
<i>Alaemon</i>	2	1		<i>Criniger</i>	5	1	
<i>Rhamphocoris</i>	1	1		<i>Pycnonotus</i>	4	2	
<i>Ammomanes</i>	3	2		TURDIDAE			
<i>Calandrella</i>	4	3		<i>Pogonocichla</i>	1	1	1
<i>Spizocorys</i>	5	1		<i>Swynnertonia</i>	1	1	1
<i>Eremalauda</i>	2	1		<i>Stiphornis</i>	1	1	
<i>Chersophilus</i>	1	1		<i>Sheppardia</i>	8	4	
<i>Galerida</i>	4	3		<i>Erithacus</i>	1	1	1
<i>Eremopterix</i>	6	2		<i>Luscinia</i>	3	3	
HIRUNDINIDAE				<i>Irania</i>	1	1	
<i>Pseudochelidon</i>	1	1	1	<i>Cossypha</i>	14	9-10	6
<i>Psalidoprocne</i>	5	3		<i>Xenocopsychus</i>	1	1	
<i>Riparia</i>	4	1		<i>Alethe</i>	5	5	1
<i>Hirundo</i>	24	9	3	<i>Neocossyphus</i>	4	4	1
<i>Delichon</i>	1	1		<i>Cercotrichas</i>	10	8	4
MOTACILLIDAE				<i>Namibornis</i>	1	1	
<i>Motacilla</i>	6	3		<i>Phoenicurus</i>	3	3	1
<i>Anthus</i>	19	1-3	1	<i>Saxicola</i>	3	2	
<i>Macronyx</i>	8	1		<i>Oenanthe</i>	17	16	3
CAMPEPHAGIDAE				<i>Cercomela</i>	8	1	
<i>Coracina</i>	4	1		<i>Myrmecocichla</i>	9	5	2

**OTIDIDAE** *Chlamydotis undulata*: vegetable matter, "small invertebrates especially ants and beetles, and small reptiles".

**CHARADRIIDAE** Lapwings *Vanellus* probably eat significant amounts of ants.

**LARIDAE** *Larus audouinii*: "Of 120 Apr-June pellets from Morocco, 87% contained fish, 5% insects . . . insects were winged ants (40%)".

**CAPRIMULGIDAE** Of 23 nightjar species, 9 are known to eat alate ants, of which these birds are probably major predators.

**APODIDAE** Of 21 species, no less than 18 eat ants, and swifts are probably even more important myrmecophages than nightjars.

**MEROPIDAE** 10 out of 18 African bee-eaters consume ants. *Merops albicollis*: Nigerian pellet samples "(n=1700 insects) were . . . ants (overall 56%)" and Ivory Coast gizzards "(n=1500 insects) were 55% ants (1 gizzard with 200 *Crematogaster* ants). Flying termites not commonly eaten". *M. orientalis*: "Airborne insects: 75% Hymenoptera . . . mainly ants". *M. malimbicus*: "Flying ants (70% of 1250 prey items,



R. Niger)". Further details of ant-eating in African bee-eaters are given by Fry (1984).

**CORACIIDAE** *Coracias* rollers may be important predators of ants, but, certainly, few African genera are more so than the broad-billed rollers *Eurystomus*. *E. gularis*: "Flying ants (91% of 3623 items in 20 stomachs, mainly *Crematogaster*, also *Oecophylla*), flying termites 3%". *E. glaucurus*: "Specialises on swarming winged ants (e.g. *Crematogaster*, *Oecophylla*) and termites (e.g. *Macrotermes*, *Pseudacanthotermes*). 1644 insects from stomachs were: ants 66%, termites 15%". "Up to 280 birds quickly assemble at a large hatch and feed . . . with swifts and swallows . . . [each catching] 6–10 [insects] per min . . . normally 200–400 and sometimes 600–800 insects" (Thiollay 1970).

**BUCEROTIDAE and CAPITONIDAE** Ground- and tree-feeding hornbills (*Tockus*, *Ceratogymna*) and ground-feeding barbets (*Trachyphonus*) may be major ant predators.

**PICIDAE** Both species of wrynecks, *Jynx*, all 10 species of the endemic woodpecker genus *Campethera*, the ground woodpecker *Geocolaptes olivaceus*, and the only African species of *Picus*, are predominantly myrmecophages. *Jynx torquilla*: "Mainly ants, up to 500 reported in 1 stomach . . . young fed on adults, pupae, larvae and eggs of ants." *J. ruficollis*: "Mainly ants, their larvae, pupae [and] eggs . . . from ant nests in the ground, also on trees . . . the small ants *Pheidole megacephala* and *Crematogaster castanea* made up c. 88% of diet (Tarboton 1976)". *Campethera punctuligera*: "Stomachs (n=25) contained only ants, their larvae and pupae, and in 5 cases, termites". *C. abingoni*: "Almost entirely ants, their pupae, larvae and eggs". The other *Campethera* species are reported in like vein, although their diets are less well known. *Geocolaptes olivaceus*: "Entirely ants (pupae, larvae, eggs, adults) of various unidentified spp.". *Picus viridis*: "Major food, ants (*Camponotus nylanderii*, *Crematogaster scutellaris*)".

**ALAUDIDAE** Six lark genera are not yet known to eat ants in Africa; 13 genera are known to, and of their 57 species, 24 (42%) take ants and 3 or more could be major predators. *Mirafrapa apiata*: "Ants . . . and . . . termites (*Hodotermes mossambicus*)". *Certhilauda curvirostris*: "Insects (termites, including *Microhodotermes viator* . . . ants *Tetramorium* and *Anoplolepis*)". *C. albescens*: ants include *Messor*, *Pheidole*, *Tetramorium*, *Crematogaster* and *Acantholepis*. *Chersomanes albofasciata*: "Insects. ♂♂ eat more tenebrionid beetles, ♀♀ more ants and harvester termites". *Spi-zocorys sclateri*: invertebrates—caterpillars, small beetles, "ants (*Messor capensis*, *Monomorium* spp.)".

**HIRUNDINIDAE** Like other small-billed aerial insectivores (nightjars, swifts), most swallows almost certainly consume large numbers of ants in Africa as they are known to do elsewhere (Turner & Rose 1989). Detailed investigations of most species have been lacking in Africa. An exception is *Hirundo spilodera*, in which the main prey are beetles, flies and wasps. Ten species of ants occurred in 4–16% of stomachs (genera *Simonopone*, *Messor*, *Pheidole*, *Solenopsis*, *Tetramorium*, *Triglyphothrix*, *Anoplolepis*, *Camponotus*) and *Camponotus maculatus* occurred in 36% of another sample (Earlé 1985). Diets of the swallows *Phedina* and *Pseudhirundo* are unknown; the 5 other genera all catch ants, and of their 35 species at least

15 (43%) do so. Major predators are *Pseudocalyptomena eurystomina*, whose diet is 65% ants, 8% other hymenopterans and 24% termites, and 2 more species of *Hirundo*. *H. daurica*: "Not studied in Africa, but in France 25-day nestlings were fed 255 items, 94% winged ants". *H. rustica*: food in Africa is very varied and includes arillate seeds. Ants feature as follows: "Small airborne insects, mainly ants, flies and beetles (25 birds, Uganda) . . . 4 birds, Orange Free State, each contained 17–120 ants [only] . . . 2 road kills, Kenya, contained . . . 22 winged ants [and 43 other insects] . . . casualties at a Zimbabwe roost had stomachs packed solid with small flying ants".

**MOTACILLIDAE** *Anthus cervinus*: "Insects and their larvae (especially ants, beetles, flies)".

**PYCNONOTIDAE** 19 out of 44 species in 8 genera are known to eat ants and 3 other genera are not yet implicated. *Andropadus* and *Phyllastrephus*, with 5 ant-eating species each, may be important. All 3 *Bleda* species eat ants. *P. terrestris*: "Arthropods, including insects . . . especially ants".

**TURDIDAE** Of the 26 African genera, only 3 (*Monticola*, *Zoothera*, *Turdus*) have not been dealt with in *The Birds of Africa* so far. Five of them are not yet known to eat ants: *Cichladusa* (with 3 species) and the monotypic *Cossyphicula*, *Modulatrix*, *Arcanator* and *Pinarornis*. Of the other 18 genera, 67 of their 91 species (74%) take ants, and 21 or more species are major predators. The endemic alethes *Alethe* habitually attend army ant swarms in forest; the 5 *Alethe* species eat some army ants (*Dorylus*), but they depend mainly on other invertebrates that the army ant columns flush. Some species of *Neocossyphus* are known as ant-thrushes and some of *Myrmecocichla* as anteater-chats, with good reason. Robins, and robin-chats *Cossypha*, are particularly important ant predators (Oatley 1970, 1992). *Pogonocichla stellata*: ants were found in 43% of faecal samples in Natal (but were outnumbered by moths and particularly beetles). *Swynnertonia swynnertoni*: "In 25 stomachs and 4 faeces (Chirinda, Zimbabwe), there were beetles in 93%, ants in 55% . . . In 20 [other] stomachs, beetles and ants made up 72%". *Erithacus rubecula*: food in North Africa has not been studied but in south Spain in one study "of > 1900 invertebrates 76% by number were ants". *Cossypha caffra*: in 104 samples mainly from Natal "ants occurred in 88%". *C. humeralis*: in 38 samples "there were beetles in 63%, ants in 55%"; this robin-chat also eats termites, spiders, fruits, etc. *C. heuglini*: in 28 samples from Zaïre, Zambia, Malawi and Zululand there were "ants (Ponerinae, Dorylinae, Camponotinae, Myrmicinae) in 86%". *C. natalensis*: in 47 samples from 5 countries there were "beetles . . . in 79%, ants in 77%" and smaller percentages of other invertebrates and fruits. *C. dichroa*: in 44 samples "from Natal and Transvaal there were beetles in 73%, ants in 61%, moths and caterpillars in 34%" etc. *C. heinrichi*: "Principally ants, including doryline driver ants". *Alethe poliophrys*: "Insects, including beetles, flies and army ants (60–80 in one stomach . . .)". *Neocossyphus poensis*: "insects, larvae and pupae (ants, including army ants; termites, beetles, grasshoppers)". *Cercotrichas quadrivirgata*: in 21 samples from Malawi and Natal there were beetles in 76%, ants in 71%, termites in 48%, etc. *C. signata*: analysis of 27 samples showed that "ants (63%),

beetles (59%), and millipedes (48%) are the most frequent prey". *C. leucophrys*: in 51 "samples from southern Africa there were: termites in 69%, ants in 67%, beetles ... in 59%", etc. *C. paena*: "In 8 stomachs (Botswana, Transvaal) there were: termites ... in 100%, beetles ... in 62%, ants (Ponerinae, Myrmicinae) in 62%", etc. *Phoenicurus moussieri*: "Insects, mainly ants, beetles, grasshoppers and larvae". Although all but one of the 17 wheatears *Oenanthe* in Africa are known to eat ants, there are few quantitative data and only 3 species seem to be major predators of ants. *Oenanthe leucura*: "Mainly insects, especially beetles and ants". *O. lugens*: "Mainly ants; also beetles, grasshoppers and other insects". *O. pileata*: "Insects, especially ants, also flies, locusts", etc. *Myrmecocichla formicivora*: "Insects, especially ants and termites. In 33 birds near Bloemfontein, South Africa, Hymenoptera (almost all Formicidae) dominated numerically in summer, and they and termites (entirely *Hodotermes*) in winter" (Earlé & Louw 1988). (The diet of *M. aethiops*, the Northern Anteater-Chat, has not been quantified; it is doubtless much like its allospecies *A. formicivora*.) *M. arnotti*: "Insects and spiders, especially ants".

## Discussion

Chapin (1953) reported that *Pseudochelidon eurystomina* feeds entirely on the wing and that stomachs contained a few Hemiptera, Homoptera, beetles, flies and small butterflies, and many alate ants. Recent observers also report that this aberrant swallow forages largely if not exclusively in flight; and Chapin's early diagnosis about its diet is amply confirmed by the present study.

Ants are an abundant, diverse, and conspicuous component of the tropical insect fauna, in savanna grassland and woodland as well as in rainforest. It is thus not altogether surprising to find that 28% (and possibly >50%) of the terrestrial bird fauna exploit them. However, it is remarkable that as many as 55 species appear to be specialist myrmecophages, a number that can only rise when information on the 864 uninvestigated passerines becomes available.

Major ant predators fall into 3 principal guilds: aerial hunting of alate ants, tree bark probing, and ground foraging on mainly non-alate ants.

Aerial predators are the nightjars, swifts, bee-eaters, *Eurystomus* rollers, and swallows. The rollers forage only at mass crepuscular swarms of ants and termites. Swifts and swallows feed at swarms, but also on dispersed flying ants and other small insects. Nightjars (crepuscular and nocturnal) and bee-eaters (diurnal) seem to feed mainly on ants and other insects that are dispersed and not swarming.

The bark-probing guild includes wood-hoopoes and 3 genera of strongly myrmecophagous woodpeckers. They forage by probing and gleaning mainly woody vegetation; they also probe ants' nests in the ground (*Picus*), and hop on the ground to glean it near the bases of trees (*Jynx*, several species of *Campethera*). Woodpeckers (Picinae), of course, provide the one avian example of gross anatomical adaptation to myrmecophagy, with their thick skin, sticky saliva, hyoid horns, and extraordinarily long, worm-like, protrusible, mobile and barb-tipped tongues.



Ground foragers include a fourth woodpecker genus, the exclusively myrmecophagous *Geocolaptes*, which feeds gregariously in large territories, using a sentry, progressing mainly by hopping. The bulbul *Phyllastrephus terrestris* is another ant-eater that forages in small groups on the ground, by hopping. Several *Tockus* hornbills search the ground by active (if rather clumsy) hopping-running. All other species in this guild are quite long-legged walkers or hoppers, like larks, pipits, robins, chats and thrushes. They may be soft-billed or hard-billed. Most ants being small, there appears to be a body-size constraint to myrmecophagy among their avian predators, with few being larger than francolins (500 g) or even than lapwings (250 g). Bustards and *Ceratogymna* hornbills, ground and arboreal foragers respectively, are exceptionally large; ants, some of which may be eaten adventitiously, do not feature to any significant extent in their diets.

### Acknowledgements

I thank R. Gabor, S. M. Head and D. Roberts who have helped in various ways with this study, and I am particularly grateful to P. Alexander-Marrack for providing the *P. eurystomina* material.

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## APPENDIX

Taxa in *The Birds of Africa* (Vols. 1–4) not implicated in ant-eating

STRUTHIONIFORMES, PROCELLARIIFORMES, SPHENISCIFORMES, GAVIIFORMES, PODICIPEDIFORMES, PELECANIFORMES, Ardeidae, Scopidae, Ciconiidae, Balaenicipitidae, *Plegadis*, *Bostrychia*, *Platalea*, PHOENICOPTERIFORMES, FALCONIFORMES, *Acryllium*, *Ptilopachus*, *Ortyxelos*, *Rougetius*, *Rallus*, *Porzana*, *Aenigmatolimnas*, *Amaurornis*, *Porphyrio*, *Gallinula*, *Fulica*, Gruidae, Heliornithidae, *Tetrax*, *Ardeotis*, *Otis*, Jacanidae, Rostratulidae, Dromadidae, Haematopodidae, Recurvirostridae, Burhinidae, *Pluvianus*, *Charadrius*, *Pluvialis*, Scolopacidae, Stercorariidae, *Rissa*, *Gelochelidon*, *Sterna*, *Anous*, Rynchopidae, Alcidae, *Treton*, *Turtur*, *Oena*, *Columba*, PSITTACIFORMES, MUSOPHAGIFORMES, *Oxylophus*, *Clamator*, *Pachycoccyx*, *Chrysococcyx*, *Ceuthmochares*, Tytonidae, *Otus*, *Jubula*, *Bubo*, *Scotopelia*, *Athene*, *Strix*, *Asio*, *Zoonavena*, *Urocolius*, Trogonidae, Alcedininae, Cerylinae, *Bucorvus*, *Gymnobucco*, *Prodotiscus*, *Melignomon*, *Lullula*, *Alauda*, *Eremophila*, *Phedina*, *Pseudhirundo*, *Tmetothylacus*, *Campephaga*, *Lobotos*, *Calyptocichla*, *Chlorocichla*, *Pyrhrurus*, Bombycillidae, Cinclidae, Troglodytidae, Prunellidae, *Cossyphicula*, *Modulatrix*, *Arcanator*, *Pinarornis*, *Cichladusa*.

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